Body-Tilt and Visual Verticality Perception During Multiple Cycles of Roll Rotation

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INTRODUCTION

In the present study, we tested spatial orientation in humans during constant velocity roll rotation. We characterize this ability by two types of measures: judgments about visual line orientation in space (subjective visual vertical, SVV) and estimates of body tilt [subjective body-tilt (SBT)]. We start this section with a brief review of important perceptual tests in the spatial-orientation domain.

Numerous studies have demonstrated that tilted subjects make systematic errors when asked to set a luminous line to the vertical in otherwise complete darkness (for review, see Mittelstaedt 1983). At large tilt angles, SVV settings in these studies deviated in the direction of body tilt (A-effect), whereas tests at small tilt angles (up to 30°) revealed almost veridical performance or small errors of opposite sign (Müller or E-effect) (Kaptein and Van Gisbergen 2004, 2005; Mittelstaedt 1983; Schöne 1964; Udo de Haes 1970; Van Beuzekom and Van Gisbergen 2000). Recently, Kaptein and Van Gisbergen (2004, 2005) described an abrupt transition from A- to E-effects at large tilt angles. To explore the possibility that a deficiency of the vestibular system causes the A-effects, Mittelstaedt (1983) designed an experiment in which he asked subjects on a tilt table to actively assume a 90° roll tilt position in total darkness and then, in that actively chosen position, to set a luminous line parallel to gravity. The results showed that almost all subjects were able to roll themselves very close to the intended 90° position. Yet, amazingly, the subsequently obtained luminous line settings deviated up to 30° from true vertical. In a similar experiment, Mast and Jarchow (1996) confirmed these findings for the visual horizontal. Recently, Kaptein and Van Gisbergen (2004) further extended the dissociation between the SVV and SBT across the entire 360° tilt range. The general picture emerging from their results is that systematic errors in the SBT were much smaller than in the SVV and lacked the steep discontinuity found in the SVV at large tilts. Furthermore, the SBT responses showed hysteresis effects, depending on which direction of rotation was used to reach the tested tilt angle. The hysteresis was not seen in the SVV.

Some studies have linked errors in the SVV to undercompensation for ocular counterroll (Pavlou et al. 2003; Wade and Curthoys 1997). Such uncorrected eye torsion may be responsible for small overcompensation errors (E-effects) at tilts <60° but works in the wrong direction to account for the undercompensation errors (A-effects) that are found at larger tilts.

Compared with the extensive literature on verticality perception during static roll tilt, studies on the SVV and SBT under dynamic conditions are scarce. Several studies have tested roll-tilt perception during sinusoidal roll tilt (Merfeld et al. 2005a,b; Park et al. 2006; Wright and Glasauer 2006). Others have tested verticality perception during earth-horizontal (Mittelstaedt et al. 1989) and earth-vertical yaw rotation (Pavlou et al. 2003) or at intermediate tilt angles (Vingerhoets et al. 2007; Wood et al. 2007). Keusch et al. (2004) undertook a dynamic roll-tilt study in which subjects were rotated from upright to just beyond horizontal and vice versa using constant velocity or constant acceleration and reported that error patterns depend on the rotation profile.

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All these studies have suggested that signals from the semicircular canals are an important factor in verticality perception. To further test this idea, we now, for the first time, compare measurements on body-tilt perception and visual verticality perception during three cycles of roll rotation at a constant rotation speed of 30°/s. This paradigm causes progressive decay of the signal from the cupula of the semicircular canal, which has a time constant of about 5 s (Fernandez and Goldberg 1971). A central storage mechanism perseveres this signal by increasing the time constant to ~15 s (Raphan et al. 1979), which implies a drop in the rotation signal of 55% after one cycle and of 90% after three cycles.

To estimate the potential effect of deteriorating canal signals, we shall now discuss the challenges facing the brain when it has to judge visual orientations in space and briefly consider the putative role of the canals in that process. Determining the orientation of a visual line with respect to space is mainly supplied by the vestibular system, which has otoliths for the detection of inertial acceleration and tilt and uses semicircular canals to sense rotations. Because the otoliths, as linear accelerometers, sense the sum of inertial and gravitational accelerations (known as gravito-inertial force, GIF), they cannot distinguish tilt and translation without further processing (Angelaki and Dickman 2000; Fernandez and Goldberg 1976; Loe et al. 1973). Recent studies have argued that the brain uses the canal signal to solve this problem (Angelaki et al. 1999; Glasauer 1992; Glasauer and Merfeld 1997; Merfeld 1995; Merfeld and Zupan 2002; Yakusheva et al. 2007; Zupan et al. 2002). Put simply, the brain interprets a change in the otolith signal as a result of tilt if the otolith signal is consistent with rotation signaled by the canals and as due to translation otherwise. Several human studies have shown that the canal-otolith interaction hypothesis provides a fair description of human perception during various motion paradigms such as centrifugation, combined tilt and translation and postrotational tilt (Merfeld and Zupan 2002; Merfeld et al. 2001, 2005a,b).

Recently, we showed that the canal-otolith interaction model proposed by Merfeld and Zupan (2002) could also explain human translation and tilt percepts during off-vertical axis rotation (OVAR) once the model was extended by the additional processing stages (leaky integrator and bias mechanism) shown in Fig. 1A (for details, see Vingerhoets et al. 2006, 2007). The core of this extended model has three output

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**FIG. 1.** A: canal-otolith interaction model with egocentric bias mechanism. Otoliths detect gravito-inertial force (GIF), the sum of inertial acceleration and gravitational acceleration, while the canals integrate angular acceleration to angular velocity. Based on canal signals, otolith signals, internal models of the sensors, and inbuilt laws of physics, the model provides estimates of the internal representation of gravity ($\vec{g}$), the internal representation of linear acceleration ($\vec{a}$) and the internal representation of angular velocity ($\vec{\omega}$). The internal representation of gravity ($\vec{g}$) drives the percept of subjective body tilt (SBT) directly. Subjective visual vertical (SVV, $\vec{g}$) is calculated as a weighted sum of subjective zenith ($-\vec{g}$) and an egocentric bias ($\vec{b}$) that pulls the estimate of verticality toward upright, i.e., $\vec{g} = -\vec{g} + w \cdot \vec{b}$. $\vec{b}$ denotes the angle between the SVV and the long-body axis and $\gamma$ represents the angular error in the SVV. C: model predictions for angle $\beta$ when a subject is rotated at 30°/s to an absolute tilt angle of 60° directly by CW rotation or by a detour CCW rotation. Internal-model parameters: $k_w = -4$, $k_\omega = 4$ s\(^{-1}\), $k_{sw} = 8$ s\(^{-1}\), and $k_{\omega \omega} = 8$. Top: without egocentric bias ($w = 0$), $\beta$ progressively lags behind as rotation continues but quickly catches up after rotation has stopped. Bottom: egocentric bias ($w = 0.5$) introduces an additional systematic error that persists after rotation stop. The bias pulls the estimate toward upright, i.e., to 360° for tilt angles >180° and to 0° for tilts <180°. D: model prediction for a static SVV experiment where a subject is tested across the whole 0–360° tilt range. Top: actual roll and angle $\beta$. Angle $\beta$ is biased toward upright. Bottom: error in SVV. Model predicts $A$-effects denoted by positive errors in the range 0–180° and negative errors for the range 180–360°.
vectors, which are variables coding internal representations (denoted by hat symbols) of the direction of gravity in a head-centric frame ($\hat{g}$), of head acceleration assigned to translation ($\hat{d}$), and of angular head rotation velocity ($\hat{\omega}$). During OVAR, involving rotation about a tilted yaw axis, an illusory percept of translation gradually develops after rotation onset. This percept could be simulated by the model when a leaky integrator was included in the translation pathway (Vingerhoets et al. 2006). Visual verticality percepts during OVAR were also accounted for by the model (Vingerhoets et al. 2007), provided that signal $\hat{g}$ was combined with an egocentric bias ($b$), with a weighting factor $w$, that effectively pulls the SVV toward the long-body axis (Fig. 1B). As our model (Fig. 1A) suggests that the egocentric bias works out similarly under static and dynamic conditions, the first objective of the present study is to explore whether errors in the SVV under dynamic conditions are comparable to those under static conditions. Our second aim is to investigate whether the dissociation of SVV and SBT performance, observed under static conditions, can be generalized to roll rotation under dynamic conditions. The working hypothesis to be tested, made explicit in Fig. 1A, holds that both tasks share the same source signal ($\hat{g}$) but that they differ in that the bias mechanism is only involved in the SVV task. As several studies have emphasized the importance of the canal signal in verticality perception, the final goal of the present study is to test how well the brain can maintain the internal representation of gravity ($\hat{g}$) during prolonged roll rotation in the dark despite the decay of the canal signals. To facilitate the interpretation of the data, we now evaluate the predictions of our canal-otolith interaction model (Fig. 1A) for verticality perception during both static and dynamic roll tilt experiments.

Model predictions

Veridical performance in the SVV test requires that $\beta$, which is the angle between the long-body axis and the SVV (see Fig. 1B), equals the actual roll-tilt angle ($\rho$). The model predicts that the computation of $\hat{g}$ lags behind due to the decay of the canal signals, which causes a difference in the SVV depending on whether the tested tilt angle was reached via a clockwise (CW) or a counterclockwise (CCW) rotation. Figure 1C, top, plots $\beta$ for a classical stationary experiment where the subject is rotated from upright to 60° roll tilt, using a direct CW rotation, and for a detour CCW rotation to the same final tilt angle, both in the absence of the bias effect ($w = 0$). Note that, in this special case without bias, the SBT predictions (not shown) would be identical. In both simulations, the SVV lags behind the actual roll tilt. This leaves a small difference between CW and CCW rotation directly after rotation stop which vanishes quickly. Thus, when testing the static SVV is delayed until some 30 s after rotation stopped, a common procedure also adopted in our static experiments, any trace of the lag in $\hat{g}$ has disappeared. For comparison, Fig. 1C, bottom, shows the simulation for the SVV with an egocentric weight of 0.5. Again the small difference between CW and CCW rotation disappears within a few seconds after rotation stop, but the A-effect introduced by the egocentric bias remains. Figure 1D summarizes the predicted outcome of a static SVV experiment for the entire 0–360° tilt range. The top panel shows angle $\beta$, whereas the bottom panel shows the error in the SVV, denoted $\gamma$ (defined as in Fig. 1B). The egocentric bias causes undercompensation for tilt, leading to positive SVV errors for rightward absolute tilt angles and negative errors for leftward absolute tilt angles. So, in summary, these simulations imply that systematic errors in static SVV experiments reflect biasing effects rather than sluggishness of the disambiguation mechanism. Because the bias mechanism does not affect the SBT, the model predicts no systematic errors in the body-tilt percept under static testing conditions.

The model makes interesting predictions about the dynamic spatial orientation percepts during rotation. For a bias weight ($w$) of 0.5, Fig. 2A presents simulations of the four output variables during three complete consecutive cycles of CW rotation (i.e., 1080°) at a speed of 30°/s. Note, first of all, that the SVV, reflected in $\beta$, shows the superposition of two error components: the cyclical effect of the egocentric bias and a phase delay reflecting the accumulating effect of signal $\hat{g}$ progressively lagging behind actual roll-tilt. The subjective body tilt (SBT) in the second panel of Fig. 2A only shows the phase delay. As a direct corollary of these lag-related errors in the SBT, the model further predicts a translation percept ($\bar{v}_x, \bar{v}_y$) that has no basis in the actual pure-rotation stimulus ($v_x = v_y = 0$). A final prediction is that the percept of roll rotation ($\hat{\omega}_y$) decays slowly from an initial value close to veridical (30°/s) down to a steady-state value of about 20°/s. Panel B, which shows the perceived head trajectory predicted by the model, will be discussed later (see Discussion).

In this study, we leave the predicted translation and angular velocity percepts aside and concentrate on testing the model’s SBT and SVV predictions. How the combination of the phase lag in $\hat{g}$ and the bias mechanism ($w = 0.5$) affects the dynamic SVV can be seen in Fig. 2C where dashed line shows $\beta$ simulations during CW and CCW rotation. Comparison with the actual tilt angle (—) reveals cyclical deviations in the form of a waxing and waning A-effect, caused by the head bias, in all three cycles of rotation. Close inspection of Fig. 2C discloses a gradually increasing phase delay in $\beta$, leveling off at ~15°, which adds an additional source of errors in the SVV. Figure 2D demonstrates how these effects work out in the SVV error ($\gamma$). The bias mechanism induces a periodical error, superimposed on an exponentially rising offset due to the gradually increasing phase lag. As shown, the phase lag leads to a negative and a positive offset for CCW and CW rotations, respectively. For comparison, solid line in this panel shows the predicted errors in the dynamic SBT ($\delta$), which reflect the phase lag.

To test if verticality perception during continuous roll-rotation can be described by the extended canal-otolith interaction model (Fig. 1A), we measured the SBT and SVV in subjects during three consecutive cycles of roll rotation at 30°/s. We examined if the predicted A-effects in dynamic conditions would actually occur and whether their magnitude would reflect the same egocentric bias as in static control experiments. In addition, we tested whether the dissociation between the SBT and SVV generalizes to dynamic roll-tilts. Finally, we explored whether our results support the model prediction that otolith disambiguation becomes imperfect, in the form of a phase lag, when canal signals are dissipating. Our results show enlarged A-effects under dynamic conditions, suggesting enhanced egocentric-
bias effects. We found no gradual deterioration of SVV performance with time, suggesting that otolith-disambiguation errors were small despite the gradual decay of canal signals. The dynamic SBT, which showed no clear evidence of the predicted accumulating phase lag either, lacked the signals. The dynamic SBT, which showed no clear evidence of the predicted accumulating phase lag either, lacked the signals. The dynamic SBT, which showed no clear evidence of the predicted accumulating phase lag either, lacked the signals. The dynamic SBT, which showed no clear evidence of the predicted accumulating phase lag either, lacked the signals. The dynamic SBT, which showed no clear evidence of the predicted accumulating phase lag either, lacked the signals.

**METHODS**

**Subjects**

Six subjects (4 male, 2 female) aged between 21 and 63 yr [31 ± 16 (SD) yr] gave written informed consent to participate in this study. All subjects were free of any known neurological, vestibular or ocular disorders. All participants except JG were naive with respect to the purpose of the experiments. Before the actual experiment began, subjects were carefully instructed about the task and got a few practice runs. They never received feedback about their performance.

**Experimental setup**

The subject was seated in a computer-controlled vestibular chair that was configured for rotation about the roll axis. The head, positioned at the rotation center, was restrained in a natural upright position using a padded helmet. The torso was secured with seat belts and adjustable shoulder and hip supports. To ensure a broad distribution of tilt-induced forces over the entire torso, subjects wore a padded breast-shoulder-plate under the seat-belt straps. The legs and feet were fixed with Velcro straps and a foot rest. Subjects did not wear earplugs so that motor noise could be heard.

In all experiments, roll rotation started from the upright position and alternated regularly between CW and CCW. Perceived head orientation is not upright after 3 complete cycles of roll rotation (head 13) due to the phase delay. C: SVV model predictions for 3 complete cycles of roll rotation. Angle $\beta$ lags behind actual roll tilt and is biased toward upright due to the egocentric bias. D: error in SVV ($\gamma$) consists of 2 contributions. Egocentric bias causes a periodical error pattern in the SVV. Phase delay causes a positive offset for CW rotation and a negative offset for CCW rotation. Error in SBT ($\delta$) is not influenced by the bias mechanism and only reflects errors due to the phase delay.
Paradigms

The SVV was tested under both static and dynamic tilt conditions in two separate series of experiments. SVV testing in all experiments relied on verbal scaling of flashed-line orientations in space as used before (Kaptein and Van Gisbergen 2005; Van Beuzekom et al. 2001). This verbal scaling method was adopted because the method of adjustment was too slow for dynamic conditions. Also an adaptive staircase method in which the orientation of the luminous line is adjusted in small steps, in consecutive runs, in the direction indicated by the subject (Vingerhoets et al. 2007), did not suffice because of the bistable percepts that occurred under dynamic conditions (see Results). From five subjects we also collected SBT estimates under the same dynamic conditions for comparison with the SVV data. All experiments took place in complete darkness. Vision was always binocular and subjects were allowed to move their eyes freely.

STATIC SVV PARADIGM. In the static experiment, subjects were rotated CW or CCW about their roll axis to a final tilt angle between 0 and 360°, which was chosen randomly at 15° intervals. Once the final tilt position was reached, there was a 30-s waiting period before testing began to allow dissipation of rotational signals.

The verbal-scaling procedure was implemented as follows. After the waiting period, the polarized light was flashed briefly for 2 ms at 2-s intervals. The subject estimated the orientation of ten sequentially flashed lines in Earth-centric coordinates, using a clock scale. For example, when the subject judged the line as earth-horizontal, with the dot on the right, the response was “15 min past (the hour)”. Generally, responses were made with an attempted precision of 0.5–1 min. To present visual line orientations across the whole 0–360° range for each tilt angle, we divided this range into 10 equal segments and drew a random line orientation from each segment without replacement. Presenting the chosen line orientations in random order forced subjects to make independent judgments and prevented repeating previous responses. The verbal responses were written down and recorded digitally to allow checking afterwards. Occasional failures to respond caused a total of ~2% of missing data.

After 10 verbal responses, the subject was rotated back to the upright position to remain there for 30 s with the room lights on until the next trial began. It took two sessions of ~45 min to collect the data from all 49 static CW and CCW tilt angles along the 360° tilt range.

DYNAMIC SVV PARADIGM. The dynamic experiment tested the subjective visual vertical during constant velocity roll rotation. Starting from upright, the subject was rotated 1140° CW or CCW, i.e., three consecutive cycles (1080°) and an additional 60° to leave the subject ≥2 s to respond in each experimental run so that data for 1080° tilt could be collected. At regular intervals during the 38-s run, the subject had to estimate line orientations using a clock scale (see STATIC SVV PARADIGM). As in the static experiment, the line orientations for a given tilt angle were presented randomly but equally spaced around the clock. The SVV was tested at 15° intervals along the entire 0–1080° tilt range. In different runs, the first flashed line was presented at 0, 15, 30, or 45° tilt and subsequently every 60°, to ensure that ultimately all 15° intervals were covered while still leaving the subject ≥2 s to respond before the next stimulus appeared. The subject was instructed to estimate the angle of the flashed line in earth coordinates at the time when it was presented. After the run was completed, the subject was rotated back to upright and was given 30 s for reorientation, with the room lights on. In most subjects it took five sessions of ~45 min to collect the data of the dynamic SVV paradigm.

To illustrate that the verbal scaling method provides consistent and reliable data in both static and dynamic experiments, Fig. 3. A and B, presents the verbal estimates of the line’s orientation in space as a function of its actual spatial orientation for one tilt angle (240°).
rotation axis, first flashed randomly between 0 and 3 s after rotation start and subsequently randomly after each 3–5 s. The flashes prompted the subject to report perceived body tilt at the time of the flash, using a clock scale, as if the body were the minute hand (Van Beuzekom and Van Gisbergen 2000). Subjects were not informed about the rotation speed to prevent that they used timing as a cue for their orientation. The verbal responses were written down by the experimenter and recorded digitally to allow checking afterward. Five of the subjects that participated in the SVV task also took part in this paradigm. It took four to five sessions of ~45 min to collect all data from each subject.

Data analysis

DEFINITION OF ANGLES. In RESULTS, responses have been plotted against the total amount of preceding rotation (Δρ) which ranges from −1080 to 1080° in the dynamic experiment and from −360 to 360° in the static experiment. CW rotations (seen from behind the subject) ran from 0 to 1080°, whereas CCW rotations started at 0 and ended at −1080°. In addition to this notation, we also use “absolute tilt” to denote the deviation from upright on a 0–180° scale. All figures showing tilt-dependent responses have been doubly-labeled with both Δρ and absolute tilt scales, where 90R and 90L indicate 90° rightward and 90° leftward, respectively. We use ρ to denote angular head position on a scale from 0 to 360°. For example, the head position shown in Fig. 4A (ρ = 120°) could have been reached by Δρ = −960, −600, −240, 120, 480, or 840°.

Response error (γ) in the flashed-line experiments, a measure for the angular error in the visual verticality percept, was defined as the difference between the actual orientation of the line in space and the corresponding verbal estimate (Fig. 4A). Errors in CW direction, seen from behind the subject, were taken positive. Accordingly, A-effects yield positive and negative γ values for right- and leftward absolute tilt, respectively. To convey other aspects of subject performance, it is more appropriate to use parameter β, defined as the angle between the SVV and the subject’s long-body axis (Fig. 1B). Response parameters β and γ are linked by β = ρ − γ. Perfect task execution requires β = ρ.

Response errors in the SBT task, indicated by δ, were defined as the angular difference between actual and reported body tilt (see Fig. 4B). Errors in CW direction, seen from behind the subject, were taken positive for easy comparison of SVV and SBT errors. If errors in the SVV were simply caused by errors in the SBT, the two error profiles would be similar.

CLUSTER ANALYSIS. As RESULTS will show, we observed two distinct SVV response clusters at large tilt angles that we denote as A- and E-cluster, in accordance with Kaptein and Van Gisbergen (2005). To partition the data points into two clusters, we used an algorithm that searches for two cluster centroids which minimize the sum of point-to-cluster-centroid distances as implemented in the function “kmeans” (Matlab 7.0 Statistics Toolbox, The Mathworks). To increase the robustness of the cluster analysis we temporarily reduced the complete data set which actually consists of multiple clusters to only two clusters by pooling data from different cycles as well as from different rotation directions (CW and CCW) and then collapsing them onto the 0–180° range. Note that this was only an intermediate step in which each data point was labeled and then returned to its original position. In subject SB, we were able to separate the clusters under static conditions using the kmeans routine, but the responses in the dynamic experiment could not be separated in this manner. In this case, we defined all data points closer to the diagonal γ = x as the A-cluster (○ in Figs. 5–7) and data points closer to y = x = −180 as the E-cluster (○ in Figs. 5–7). These A- and E-clusters in Figs. 5–7 will be discussed in more detail in RESULTS.

Model simulations

Model simulations were run to find the bias weights (wE for E-cluster, wA for A-cluster) that provided the best fits to the data. For this purpose, we used Matlab 7.0 and Simulink 6.0 (The Mathworks) to simulate the canal-otolith interaction model outlined in Fig. 1A. This scheme was used previously in Vingerhoets et al. (2007) to describe verticality perception during OVAR. The core of the scheme, the internal model, was originally proposed by Merfeld and Zupan (2002). Simulations were performed using the same internal model parameters $k_x = −4 \text{s}^{-1}$, $k_y = 4 \text{s}^{-1}$, $k_w = 8$, and $k_{w_0} = 8$ that were found to be optimal in Vingerhoets et al. (2007). These four parameters are used in an iterative process in the internal model to obtain the optimal estimates of the motion variables. The linear acceleration error gain ($k_a$) controls the central estimate of linear acceleration. A negative value for this parameter ensures that force detected by the otoliths is transformed into acceleration. The GIF feedback gain ($k_{gi}$) determines how the angular difference between the estimated and measured GIF direction induces the internal sense of gravity to align with the gravito-inertial force measured by the otoliths. Likewise the angular velocity feedback gain ($k_{wa}$) determines how the difference between the estimated and the sensed semicircular canal signal influences the central estimate of angular velocity. The remaining feedback gain ($k_{wa}$) determines the central estimate of angular velocity because the path containing $k_{wa}$ monitors the angular difference between the measured GIF and the estimated GIF. In this way, $k_{wa}$ plays a critical role in keeping track of the direction of gravity and maintaining a central estimate of angular velocity. Increasing this parameter substantially can decrease the phase delay in the model predictions (Fig. 2, C and D) but cannot be tuned to simulate a phase lead.

![Fig. 4. Definition of angles with subject in rear view. Tilt position (ρ) is 120° in both panels. A: error in SVV (γ in deg) is defined as actual line orientation (STIM) minus estimated line orientation (RESP). B: response error in the subjective body tilt paradigm (δ) is defined as actual (Z) minus reported tilt angle (SBT). The example shows tilt underestimation.](http://jn.physiology.org/TOC/vol99/i5/2269cover.jpg)
In the simulations, angle $\theta$ was calculated as $\theta = \arctan(\hat{g}/\hat{g}_z)$, where $\hat{g}$ denotes the vector sum of the subjective zenith ($-\hat{g}$) and the weighted bias vector (i.e., $\hat{g} = -\hat{g} + w \cdot \hat{b}$, see Fig. 1B). The predicted error in the SVV was calculated as $\gamma = \rho - \beta$. The predicted error in the SBT ($\delta$) was obtained using $w = 0$ in the same equations. In results, the only free parameter when fitting the model to the data is egocentric bias weight $w$ ($w_E$ for E-cluster, $w_A$ for A-cluster).

RESULTS

We first measured the accuracy of the SVV at static tilt angles separated by 15° intervals along the entire 0–360° range. These data served as a baseline for comparison with the dynamic SVV at the same tilt angles in each of three consecutive cycles of roll rotation. We also collected SBT estimates under the same dynamic conditions to explore if errors in visual verticality perception can be attributed to errors in tilt perception.

Overview of main findings

RESPONSE MEASURES. To introduce our results, Fig. 5 plots both compensation angle $\beta$ and response error $\gamma$ during static and dynamic tilt in subject SV. Although our verbal scaling method is less precise than classical adjustment methods, we obtained firm results with a clearly delineated pattern of responses. In the case of flawless performance, all data in obtained firm results with a clearly delineated pattern of respective compensation cycles of roll rotation. We also collected SBT estimates under the same dynamic conditions to explore if errors in visual verticality perception can be attributed to errors in tilt perception.

STATIC SVV. Our complete static data set shows a similar pattern of A- and E-effects in different tilt ranges, for both CW and CCW rotation, in all subjects. As similar data has been presented earlier (Kaptein and Van Gisbergen 2005) and a repeated-measures two-way ANOVA on the A-cluster data showed no significant main effect of the preceding rotation direction [$F(1,5) = 0.58, P = 0.48$] and no significant interaction between tilt angle and rotation direction [$F(16,80) = 0.003, P = 1$], we now only provide the results of our static CW data in Fig. 6 (left). The fit line through the data will be discussed later (see Model fits to experimental data). All subjects demonstrated A-effects that increased steadily for tilt angles up to $\approx 135°$. Beyond this range, five of six subjects showed an abrupt transition from A- to E-effects with again a sudden return to A-effects around 225°. This A-E dichotomy was less clear in subject MV. The strong impression of two

![Fig. 5. Static and dynamic SVV results from subject SV. Data from clockwise (CW) rotation. Different symbols show the result of the cluster analysis. A: angle $\beta$ (Fig. 1B) in static experiment. Ideal behavior requires $\beta = \rho$ (---). A-cluster (⊙) responses are biased toward upright (0 and 360°); E-cluster (●) responses are biased toward 180°. B: angle $\beta$ in dynamic experiment. Initially $\beta = \rho$, later there are A- and E-effects. C: SVV errors in static experiment. Near the inverted position (150–225°) E-effects occur. The remaining tilt range shows A-effects. D: errors in SVV in dynamic experiment. In the first 90° errors are rather small. Subsequently, errors show a repeating pattern of A- and E-effects in successive cycles.](http://jn.physiology.org/ by 10.2203.33.5 on June 28, 2017)
distinct response modes was confirmed by cluster analysis (kmeans, see METHODS), which yielded clearly delineated A-effect (○) and E-effect (●) clusters in all subjects. This analysis established that the A-response mode prevailed for tilt angles up to \( \sim 135^\circ \) and that the E-effect mode was dominant for tilt angles near upside down. Note the sharp demarcation between A and E cluster in most subjects with no clear sign of bimodal responses. The latter finding may be related to the fact that all

![Comparison of static and dynamic results. In this and following figures, the horizontal axis is doubly labeled. The bottom scale denotes the amount of rotation imposed on the subject. The labeling on top denotes absolute tilt angle, the deviation from upright. Left: errors in static subjects, tested after CW rotation. Right: errors in the 1st dynamic CW cycle. In both paradigms there is a clear A-effect that dominates in the range of absolute tilt angles up to \( \sim 135^\circ \). Errors in the A-cluster are generally larger in the dynamic paradigm. At large absolute tilts, a response of the E-type emerges. In the dynamic paradigm, the tilt range of E-type responses is larger and shifted to the left. Static responses are mostly unimodal at a given tilt angle; dynamic responses at near inverted tilt are often bimodal (A and E). Solid lines, model fits.](http://jn.physiology.org/)

FIG. 6.
data points at a given tilt angle were obtained in a single trial. Kaptein and Van Gisbergen (2005) found that subjects seldom switch response mode within one trial.

DYNAMIC SVV. To allow a direct side-by-side comparison of static and dynamic results, Fig. 6 presents CW data from the static experiment and from the first cycle of the corresponding dynamic experiment. The response patterns for static and dynamic, both showing a steadily increasing A-effect with tilt angle and an E-effect in the near upside down region, look qualitatively similar. However, closer inspection reveals clear quantitative differences. First, several subjects show larger A-effects in the dynamic experiment. This difference is very marked in subject SB, who shows only limited errors in the static condition but makes errors up to 180° in the dynamic paradigm. Thus when in the A-response mode, lines directed toward the floor were sometimes misperceived as pointing upward. The smooth increase of dynamic errors with tilt angle in SB and JG suggests that the responses at 180° are not simply due to line-polarity misjudgments. In qualitative terms, this effect can be explained as follows. Under dynamic conditions, the bias in these subjects becomes so strong that their evaluation of the line is almost equivalent to performing the task in body coordinates, with hardly any effect of the degree of body tilt. As long as body tilt is small or modest, the direction of gravity is still almost aligned with the body axis so that the body-associated bias is not so obvious. However, this leads to errors of 180° in the extreme case that the two references (gravity, body) are in opposition. A further noticeable difference is that there is less intersubject variability in the static paradigm. For example, subjects JG and SV show similar error profiles in the static paradigm but quite different patterns in the dynamic paradigm. Another clear difference between the static and dynamic results concerns the E-cluster. In the static paradigm, the E-cluster is approximately symmetric around 180°, between 120 and 240°, but in the dynamic paradigm, it has shifted to smaller tilt angles, between 90 and 195° in most subjects. A similar asymmetry in the tilt range with E-responses can be seen in CCW responses (see Fig. 7). A final outstanding difference highlighted by Fig. 6 is that the relatively sharp tilt boundaries between A- and E-clusters in static results disappear under dynamic conditions. In the dynamic paradigm, the A and E-clusters occupy overlapping tilt ranges so that the response distribution becomes bimodal. That two responses modes may coexist at certain large tilt angles has been reported earlier by Kaptein and Van Gisbergen (2005). We cannot exclude that this difference has its origin in the testing method. Subjects were statically tested 10 times within a single run, but dynamic data at a given tilt angle were collected in separate runs.

What is the effect of prolonged rotation on the SVV in later cycles? Recall that the canal-otolith interaction model (Fig. 1A) cannot fully sustain the tilt signal, due to the decay of canal signals (see Fig. 2C), causing the predicted dynamic SVV to be different in the first, second and third rotation cycle (Fig. 2D). The actual data from all three cycles for both CW and CCW rotations, shown in Fig. 7, rather indicate a roughly repeating pattern of A- and E-clusters for all subjects without clear signs of a phase shift. For a quantitative analysis of the phase-lag issue, see Analysis of phase shifts. The A-clusters are centered around the upright positions, whereas E-cluster responses dominate around the inverted tilt positions. However, note that the E-cluster is shifted to smaller tilt angles as we already observed in Fig. 6.

Close scrutiny of the initial part of the first cycle, ≤90°, reveals smaller errors than in the corresponding tilt ranges in subsequent cycles, but the responses during the second and third cycles are virtually identical. We tested this onset effect by pooling CW and CCW data and comparing responses from the tilt range 0–90° in the first, second, and third cycle in a two-way ANOVA with tilt angle and cycle as factors. We found no significant interaction [F(12,105) = 0.99; P = 0.46] but a significant main effect of both tilt angle [F(6,105) = 35.15; P < 0.01] and cycle [F(2,105) = 4.88; P < 0.01]. Tukey’s post hoc test revealed that these errors in the second and third cycle of rotation were not significantly different but both were significantly larger than those in the same range of the first cycle of rotation, confirming the existence of a clear onset effect.

DYNAMIC SBT. In a final experiment, we tested subjects in the SBT paradigm, where they verbally reported their current body tilt estimate on a clock scale, when prompted by a LED flash (see METHODS). Figure 8 plots the difference (Θ, see Fig. 4B) between the absolute tilt angle and the estimated tilt angle for all five tested subjects. Mean errors are much smaller than in the dynamic SVV paradigm, showing no convincing overall resemblance with the tilt-related pattern of errors in the SVV task (Fig. 7). To investigate this further, we calculated correlations between SBT errors, separately for the A- and E-clusters, and the SBT data. The correlation was only significant in subject SP, indicating a clear dissociation of performance in the two spatial orientation tasks at the population level.

Most subjects tend to show tilt overestimation in the first 90° after rotation onset (positive errors for CCW and negative errors for CW). This impression was confirmed by a two-way ANOVA with tilt angle and cycle as factors, which revealed a significant main effect of rotation cycle [F(2,105) = 14.06; P < 0.01]. Tukey’s post hoc test showed that SBT errors in the selected tilt range (0 to 90°) in the second and third cycles of rotation were indistinguishable but significantly different from those in the same range in the first cycle of rotation by showing underestimation. In this sense, the onset effect observed in the SVV data has a parallel in the SBT data. From the perspective of the model, the fact that an onset effect showed up in both the dynamic SVV and SBT data may indicate that it is already present in signal , but its origin remains unclear. One could speculate that it was caused by activation of the vertical semicircular canals (Jaggi-Schwarz and Hess 2003; Jaggi-Schwarz et al. 2003; Keusch et al. 2004; Pavlou et al. 2003) or that a computational delay, which is not incorporated in the model, is involved (see DISCUSSION, Disambiguation process).

In some subjects (e.g., SP), the error pattern in the SBT looks periodic. To analyze this in more detail, we averaged the data in bins of 15° and pooled across subjects. This yielded a pattern that was roughly similar for CW and CCW rotation as shown in Fig. 9. For both rotation directions, the error in SBT starts at a negative value, which indicates overestimation of tilt and corresponds to the onset effect described above. Subsequently the error reverses sign and increases, but resets at 360° tilt. Then the error increases again in the next cycle and returns to zero at 720° tilt. Also the third cycle shows this character-
FIG. 7. Error profiles of the dynamic SVV in all subjects. Comparison of results from CW and counterclockwise (CCW) rotation. CW plots should be read from the center to the right; CCW responses from the center to the left. Although errors just after rotation onset appear smaller than in later cycles, there is a repeating response pattern across sequential cycles. Solid lines, model fits to dynamic A-clusters have bias weights that are larger than in static conditions (compare Tables 1 and 2). Fitting E-clusters requires negative bias weights. Note that E-clusters in CW and CCW are shifted in opposite directions, indicating a clear phase shift.
istic, suggesting that subjects develop a slight phase lag during each cycle, that resets at upright. This is reminiscent of results from Kaptein and Van Gisbergen (2004). The reset at upright deviates from the model prediction of steadily increasing errors previously shown in Fig. 2D and replicated here and may reflect factors not included in the model such as somatosensory cues.

Model fits to experimental data

STATIC SVV FITS. We used the extended canal-otolith interaction model shown in Fig. 1A to fit the weight of the egocentric bias separately to the A- and E-cluster data from each subject. The fit, indicated by — in Fig. 6 (left), was made on CW and CCW data simultaneously. Overall, the fits capture the A-effects quite well except that in some subjects (JG and SV), the slope of the model fit is somewhat too steep at small tilt angles and slightly too small for larger tilt angles. The figure also shows that the separate fit of the model to the E-cluster provides a good description of this response mode. The best fit bias weights for the A- and E-clusters can be found in Table 1 which also lists the root mean squared error (RMSE) and $R^2$ values of the fits. For the A-cluster, individual bias weights range from 0.27 to 0.92 (mean ± SD: 0.54 ± 0.24), indicating

FIG. 8. Dynamic SBT task. Systematic errors are generally small, and there are no indications of a tilt-dependent pattern of errors as in the SVV.
that the estimated direction of gravity is on average about twice as important in the SVV computation as the egocentric bias. RMSE values range from 10.1 to 18.4° (13.0 as important in the SVV computation as the egocentric bias. Model prediction (thin line) shows a steadily increasing underestimation error. Sign of CCW errors was inverted to allow comparison with CW data.

**TABLE 1. Individual weights of the egocentric bias and RMSE and $R^2$ values for the static SVV fits**

<table>
<thead>
<tr>
<th>Subject</th>
<th>$w_A$</th>
<th>RMSE, deg</th>
<th>$R^2$</th>
<th>Subject</th>
<th>$w_E$</th>
<th>RMSE, deg</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>JG</td>
<td>0.92 ± 0.02</td>
<td>13.4</td>
<td>0.87</td>
<td>JG</td>
<td>-10</td>
<td>16.0</td>
<td>0.69</td>
</tr>
<tr>
<td>JW</td>
<td>0.49 ± 0.01</td>
<td>11.2</td>
<td>0.75</td>
<td>JW</td>
<td>-19 ± 0.4</td>
<td>13.4</td>
<td>0.67</td>
</tr>
<tr>
<td>MV</td>
<td>0.36 ± 0.02</td>
<td>14.0</td>
<td>0.51</td>
<td>MV</td>
<td>0.19 ± 0.04</td>
<td>17.4</td>
<td>0.10</td>
</tr>
<tr>
<td>SB</td>
<td>0.27 ± 0.02</td>
<td>18.4</td>
<td>0.25</td>
<td>SB</td>
<td>-0.8 ± 0.2</td>
<td>18.4</td>
<td>0.38</td>
</tr>
<tr>
<td>SP</td>
<td>0.72 ± 0.02</td>
<td>10.1</td>
<td>0.88</td>
<td>SP</td>
<td>-2.4 ± 0.5</td>
<td>14.3</td>
<td>0.57</td>
</tr>
<tr>
<td>SV</td>
<td>0.50 ± 0.02</td>
<td>11.1</td>
<td>0.76</td>
<td>SV</td>
<td>-1.1 ± 0.2</td>
<td>12.2</td>
<td>0.60</td>
</tr>
</tbody>
</table>

Fit parameter $w_E$ was bounded at -10 because decreasing it further did not improve the fit.

**FIG. 9.** Errors in dynamic SBT task averaged and pooled across subjects. Error patterns for CW (thick line) and CCW (dashed line) are similar. Both patterns start with a negative offset and then increase up to 10°. After 1 cycle, errors reset and then gradually increase again. Same pattern in the 3rd cycle. Model prediction (thin line) shows a steadily increasing underestimation error. Sign of CCW errors was inverted to allow comparison with CW data.

**FIG. 7 (see also Table 2).** The dynamic bias weights in both clusters exceed the static values in all subjects. Individual bias weights range from 0.97 to 3.9 (1.63 ± 1.12) for the A-cluster and from −10 to −1.8 (−4.27 ± 3.02) for the E-cluster. These larger dynamic bias weights suggest that the body axis is more dominant as a partial reference for verticality judgments than in static tilts. A possible explanation for this phenomenon will be presented in Bayesian perspective on the bias effect in discussion. Table 2 shows that RMSE values are approximately twice as large as in the static paradigm, which is mainly due to the increased scatter in the responses. As indicated by the comparable $R^2$ values, the average error pattern is still fitted quite well. Thus the analysis shows that the model in Fig. 1A can account quite well for both the static and dynamic SVV data if we allow different egocentric biases for these two conditions as well as for the A- and E-cluster.

**DYNAMIC SBT FITS.** To test whether the egocentric bias mechanism only affects the SVV, without influencing the SBT estimates (see Introduction), we also fitted the bias weights to the dynamic SBT data. This resulted in bias weights ranging from −0.02 to 0.2 (0.05 ± 0.09) with only the bias weight in subject SB significantly different from zero. These results support the notion that the egocentric bias mechanism is not part of the body-tilt estimation pathway (see also Fig. 1A).

**Analysis of phase shifts**

As mentioned in the Introduction, several studies have suggested that canal signals are crucial to discriminate tilt and translation from the inherently ambiguous otolith signal. Along this line, the canal-otolith interaction model (Fig. 1A) implies that when the canal signal decays, the brain has problems compared with the static fits. With this increased bias weight, the model can even account for the errors up to 180° seen in subjects JG and SB. In the other subjects, the fit to the A-cluster in the range 0 to 180° overestimates the errors that were actually observed. This effect occurs because the fit is based on data from all three cycles and errors in the first 90° are somewhat smaller than those in later cycles, as we confirmed statistically above. Apart from this, Fig. 7 shows that the overall fit provides a fair description of the dynamic data. Except for the onset effect in the first 90°, the A- and E-cluster pattern repeats itself in successive cycles. Note that there are no clear signs of an upward trend for CW rotation and a downward trend for CCW rotation corresponding to the phase lag predicted by the model (see Fig. 2D). A more thorough analysis of the phase-lag issue follows in the next section.

The best-fit bias weights are listed in Table 2. The dynamic bias weights in both clusters exceed the static values in all subjects. Individual bias weights range from 0.97 to 3.9 (1.63 ± 1.12) for the A-cluster and from −10 to −1.8 (−4.27 ± 3.02) for the E-cluster. These larger dynamic bias weights suggest that the body axis is more dominant as a partial reference for verticality judgments than in static tilts. A possible explanation for this phenomenon will be presented in Bayesian perspective on the bias effect in discussion. Table 2 shows that RMSE values are approximately twice as large as in the static paradigm, which is mainly due to the increased scatter in the responses. As indicated by the comparable $R^2$ values, the average error pattern is still fitted quite well. Thus the analysis shows that the model in Fig. 1A can account quite well for both the static and dynamic SVV data if we allow different egocentric biases for these two conditions as well as for the A- and E-cluster.

**DYNAMIC SBT FITS.** To test whether the egocentric bias mechanism only affects the SVV, without influencing the SBT estimates (see Introduction), we also fitted the bias weights to the dynamic SBT data. This resulted in bias weights ranging from −0.02 to 0.2 (0.05 ± 0.09) with only the bias weight in subject SB significantly different from zero. These results support the notion that the egocentric bias mechanism is not part of the body-tilt estimation pathway (see also Fig. 1A).
keeping track of the direction of gravity, which leads to a phase delay in the tilt percept that can best be seen at the zero crossings of the simulation in Fig. 2C. To test whether the data actually show this phase shift, we examined the SVV estimates near the upright positions (Δρ = ±360°, ±720°). If there is in fact no phase shift, one expects SVV estimates to be aligned with the long-body axis (β = 0) when the subject is upright (ρ = 0), independent of the subject’s bias weight. On this basis, we estimated the phase shifts by determining at which tilt angle the zero crossing predicted by the model occurs when the actual tilt angle is about 10° (i.e., when Δρ = 370°) or 15° (Δρ = 735°). For CCW rotation, the effect is symmetric: β = 0 when the absolute tilt angle is 10° (Δρ = −370°) or 15° (Δρ = −735°). Middle: angle β and fit lines for subject JW around zero-crossings. Bottom: fit lines from all subjects. Zero-crossings are not shifted in the predicted direction.

This lack of evidence for a substantial phase shift in the A-cluster, contrasts with Fig. 6 where we observed that the A-cluster range was shifted to smaller tilt angles under dynamic conditions as compared with static conditions. The E-cluster starts approximately at 135° and ends at ~225° under static conditions, while dynamically the E-cluster lies roughly between 90° and 195°, which is a shift of ~30–45°. Possible explanations of this observation will be explored in the DISCUSSION (see Disambiguation process).

Finally, to investigate the possibility of a phase lag in the SBT results, we plotted the model prediction for δ superimposed on the pooled data in Fig. 9. The model predicts a monotonically increasing phase lag over the course of the three rotation cycles. Clearly, the data do not match this prediction in all aspects. First of all, it seems as if the data show a vertical shift of ~10° with respect to the model prediction. In addition, while the phase tends to increase with rotation angle, the data

![Figure 10](http://jn.physiology.org/)

**Table 2. Individual weights of the egocentric bias and RMSE and R² values for the dynamic SVV fits**

<table>
<thead>
<tr>
<th>Subject</th>
<th>wₓ</th>
<th>RMSE, deg</th>
<th>R²</th>
<th>wₓ</th>
<th>RMSE, deg</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>JG</td>
<td>3.9 ± 0.2</td>
<td>17.5</td>
<td>0.96</td>
<td>−10</td>
<td>20.4</td>
<td>0.89</td>
</tr>
<tr>
<td>JW</td>
<td>0.99 ± 0.01</td>
<td>29.9</td>
<td>0.29</td>
<td>−3.5 ± 1.2</td>
<td>28.1</td>
<td>−0.16</td>
</tr>
<tr>
<td>MV</td>
<td>1.21 ± 0.02</td>
<td>24.9</td>
<td>0.70</td>
<td>−1.8 ± 0.1</td>
<td>23.9</td>
<td>0.43</td>
</tr>
<tr>
<td>SB</td>
<td>1.60 ± 0.04</td>
<td>24.9</td>
<td>0.89</td>
<td>−1.9 ± 0.4</td>
<td>33.9</td>
<td>0.41</td>
</tr>
<tr>
<td>SP</td>
<td>1.13 ± 0.02</td>
<td>29.5</td>
<td>0.72</td>
<td>−4.6 ± 1.7</td>
<td>38.8</td>
<td>0.39</td>
</tr>
<tr>
<td>SV</td>
<td>0.97 ± 0.02</td>
<td>25.4</td>
<td>0.31</td>
<td>−3.9 ± 0.6</td>
<td>25.9</td>
<td>0.41</td>
</tr>
</tbody>
</table>

Fit parameter wₓ was bounded at −10 because decreasing it further did not improve the fit.
also show phase resets around the upright positions, which are not predicted by the model. In the DISCUSSION, we will elaborate on possible underlying mechanisms of these observations.

DISCUSSION

Research questions and main findings

We studied the accuracy of two distinct spatial orientation percepts—the SVV and the SBT—during three cycles of continuous roll rotation. For comparison, we also collected static SVV measurements. Model simulations (Figs. 1 and 2) led us to expect the following results. 1) A cyclical pattern of gradually waxing and waning A-effects in the SVV task, linked to the egocentric bias. Because the bias mechanism was assumed to be static, the model predicts a similar pattern for dynamic and static roll tilts. 2) Because the bias mechanism is only engaged in the SVV computation, the model predicts that these effects have no parallel in the SBT data. 3) Last, we expect a gradually increasing phase lag in both SVV and SBT percepts caused by imperfections of the disambiguation stage when the canal signal decays.

The first model prediction was not borne out by the data: while our SVV findings bear obvious signs of the operation of a mechanism that biases visual verticality percepts to the long-body axis, it is all too clear that the notion of a fixed bias is untenable. The fact that subjects showed larger A-effects in the dynamic experiments than in the static experiments shows that the bias effect can vary, depending on circumstances. A possible interpretation of this finding will be discussed in the following text (see Bayesian perspective on the bias effect). The emergence of the E-cluster at large tilts, both in the dynamic and static experiments, presents a further challenge. The interpretation of this phenomenon as a shift in the egocentric reference frame at near-inverse tilts (Kaptein and Van Gisbergen 2004, 2005) will be subject of discussion in the next section.

Comparison of the two dynamic data sets revealed that the second model prediction was closer to the mark. Strong signs of egocentric biasing in the SVV were virtually lacking in the SBT judgments. This remarkable difference in performance lends support to the notion that these percepts reflect different processing of a shared tilt signal (see Fig. 1A). Finally, neither the SVV findings (Fig. 10) nor the SBT data (Fig. 9) showed clear evidence of an accumulating phase delay in the course of prolonged rotation. This finding, suggesting that disambiguation errors were small in the present conditions, will be discussed later (see Disambiguation process).

Tilt-related bias

Using the egocentric bias mechanism in combination with the canal-otolith interaction model (Fig. 1A), we simulated the SVV during static and dynamic roll tilt. In its simplest form, with a single bias weight, the model predicts that the error in the SVV gradually increases up to absolute tilts of ~135° and then gradually decays back to zero at 180° tilt under static conditions (Fig. 1D). However, our data clearly contradicted the model prediction by showing an abrupt switch from A- to E-effects at large tilt angles. To account both for A-effects for tilt angles up to ~135° and E-effects at large tilt angles, we had to adopt different weight values (w) with opposite sign. The fact that fitting the E-cluster requires a switch to a negative bias weight implies that the egocentric bias, normally directed toward the head, can flip to the feet.

As has been reported before (Kaptein and Van Gisbergen 2005), this intriguing reversal from A- to E-responses, now also confirmed under dynamic conditions, can be understood as a shift in reference frame. According to this account, in most of the tilt range subjects judge line orientation in space by adding retinal line orientation to the deviation of head orientation from upright. When the amount of head tilt is undercompensated, this gives rise to an A-response. By definition, a straightforward interpretation of E-responses indicates overcompensation for tilt, but it would be hard to understand why the brain would suddenly shift from undercompensation to overcompensation. With this in mind, Kaptein and Van Gisbergen (2005) suggested the more coherent explanation that in the E-response mode, which only occurs at large tilt, the subject is again undercompensating, but now using the deviation of the feet from upright as the measure for body tilt. The present dynamical results, showing large E-effects in subjects with an on average almost veridical SBT response, fit better with this notion of a reference shift than with the earlier hypothesis (Kaptein and Van Gisbergen 2004) that E-responses may use the body tilt signal as such without the bias characterizing A-responses.

Kaptein and Van Gisbergen (2005) reported that subjects were aware of using different approaches to the task at small and large tilt angles, one more automatic the other more cognitive, respectively. At the transition zone where both A- and E-responses occurred in different trials, their report of which approach had been used (forced-choice) corresponded closely to the response mode (A or E) obtained in a particular trial (see Fig. 9 in Kaptein and Van Gisbergen 2005). When in the A-response mode, subjects have a vivid awareness of the cardinal axes of external visual space and can perform the task easily without consciously considering how they are tilted. At large tilt, this automatic awareness of visual space is lacking, forcing the subject to solve the task of combining the body tilt signal and the retinal signal at a more cognitive level. Under such conditions, the direction of “up” is derived indirectly from the feeling of being tilted at a very large angle induced by strong somatosensory cues. Based on this awareness, the brain prompts an SVV setting close to the upward pointing feet. Small sensed deviations from inverted tilt then guide small adjustments relative to this reference. If this account is accepted as a preliminary explanation of the data, the question remains how the sudden shift comes about. One might speculate that the system is designed for a limited tilt range and simply cannot cope with the rarely encountered large tilt angles, but this leaves unexplained why A- and E-modes showed considerable overlap in some subjects. This problem, and questions concerning the underlying physiological mechanisms, remain topics for future investigation.

We observed that different bias strengths were necessary to account for the A- and E-clusters in the static data. In addition, these bias weights had to be increased to fit the larger errors in the dynamic paradigm. The latter finding is a contrast with our OVAR study (Vingerhoets et al. 2007) where we found an almost one-to-one relation between static and dynamic A-effects. Moreover, the weights found in the present study, both statically (0.54 ± 0.24) and dynamically (1.63 ± 1.12), are...
Bayesian perspective on the bias effect

So far we sidestepped the problem of which mechanism may cause the SVV to be a compromise between the true direction of gravity and an egocentric reference frame, using the egocentric bias vector to quantify the effect. This pragmatic approach has been adopted before in various studies (Dyde et al. 2006; Groen et al. 2002; Haslwanter et al. 2000; Zupan and Merfeld 2005; Zupan et al. 2002). However, an important question relates to the origin of this bias. Mittelstaedt (1983, 1986, 1999) proposed that the egocentric bias serves to correct for putative systematic errors in the tilt signal caused by unequal numbers of hair cells in the saccule and the utricle. However, this interpretation would require further assumptions to explain the results of the present SBT experiments, in which the dynamic tilt estimates from our subjects were quite good, by comparison, with no signs of major systematic errors. Earlier static studies (Bortolami et al. 2006a,b; Kaptein and Van Gisbergen 2004; Mast and Jarchow 1996; Van Beuzekom and Van Gisbergen 2000) have also demonstrated that body-tilt estimates show only modest deviations from true body tilt. Furthermore, Mittelstaedt’s notion that the idiotropic vector is a fixed idiosyncratic constant contrasts with our finding that the dynamic results indicate an increased egocentric-bias weight.

We are now faced with a peculiar situation. Under dynamic conditions, the SBT, which can be seen as a reflection of the internal representation of gravity, seems quite accurate. Yet in a different task, large errors in the SVV point to an egocentric bias mechanism. Ironically, it would therefore appear as if an almost veridical internal representation of gravity is spoilt by an egocentric bias. How can this make sense? A way out of this conundrum may come from an alternative modeling approach that reinterprets the egocentric bias in terms of a tilt prior in a Bayesian observer model (Eggert 1998; MacNeilage et al. 2006; Groen et al. 2002; Haslwanter et al. 2000; Zupan et al. 2002). In this guise, the bias mechanism becomes an element in an optimal strategy to handle noisy tilt signals. The basic idea is that when there is no sensory tilt signal, the brain makes a conservative a priori assumption that the head is usually upright. This a priori assumption can then be overruled by sensory evidence. In case of weak evidence, the brain still relies mostly on the prior belief. However, when the sensory signal becomes more reliable, the brain will assign more weight to information from the sensors. The result of the combination of prior information and sensory information is that the final percept is very stable when the prior and the sensory information are compatible, in this case, for tilt angles close to upright. This is useful when the brain has to combine the relatively noisy tilt information with the very precise retinal information about line orientation. As these small tilt angles occur most often, this would be a smart strategy to optimize performance during daily life. The downside of this computational strategy is that it goes at the expense of systematic errors at large tilt angles that occur only rarely in everyday life.

But why then is the prior only used for the SVV and not for body tilt estimation? A speculative explanation is that precision is more important for the visual system than accuracy for reasons of visual stability. Thus to allow a stable perception of the visual world, noise in the tilt signal is reduced by combining it with a prior. For the percept of body tilt, it is probably less important to be precise and more useful to be accurate and therefore the prior does not take part in this process. This hypothesis is in line with remarkable findings by Mast and Jarchow (1996), who showed that body tilt adjustments to a 90° horizontal position, in the dark, are more noisy than SVV settings at the same tilt angle.

From a Bayesian perspective, the larger systematic errors in the SVV for the dynamic paradigm can be explained by a noisier tilt signal under these conditions, for example as a result of a lack of integration time. According to Bayes’ rule, a noisier tilt signal leads to more weight of the prior and thus to a final estimate that will be biased more toward upright. Hence a noisier tilt signal leads to a stronger bias. In addition, it is conceivable that the physiological internal model is less reliable in seldom experienced orientations (e.g., upside down) thus leading to more weight for the prior and a larger bias. This is consistent with our finding that the bias weights of the E-cluster were larger than the bias weights of the A-cluster. It remains a topic for further study to see if this Bayesian approach is a realistic modeling perspective.

Disambiguation process

Because gravitational and inertial acceleration forces are physically indistinguishable, the otolith signal is ambiguous (Angelaki and Dickman 2000; Fernandez and Goldberg 1976; Loe et al. 1973). Thus to mediate reliable spatial orientation, neural strategies must exist to solve the inverse problem of determining which combination of tilt and translation has led to a given otolith signal. Here we evaluated the canal-otolith interaction hypothesis as one such strategy proposed in the literature. This hypothesis, implemented in the model shown in Fig. 1A, suggests that the brain uses internal models that incorporate canal signals to solve the ambiguity problem. But even when canal cues dissipate, for example, during prolonged rotation in the dark, this model predicts that humans are still able to retain a reasonable internal representation of the direction of gravity. The model achieves this by comparing the measured GIF and the estimated GIF and using this angular difference as an additional estimate of roll rotation. As a consequence, the decay of the canal signal only results in a phase shift of the internal representation of gravity with respect to the actual direction of gravity. According to the model and the parameters we have chosen, this phase shift does not exceed 15° for the present stimulus conditions.

If our model, suggesting that $ \tilde{g} $ is the source signal for SVV and SBT, is correct, both should have an accumulating phase shift. However, in the present stimulus conditions, neither SVV nor SBT showed clear signs of a monotonically increasing phase shift. To conclude that otolith disambiguation was almost perfect under the present experimental conditions would be a marked contrast with our earlier OVAR studies (Vingerhoets et al. 2006, 2007) where, in line with the model predictions, illusory translation and tilt underestimation occurred as a result of imperfect otolith disambiguation. The question is how...
this discrepancy can be explained. The model is quite consistent in predicting a similar phase delay for both OVAR and roll rotation. In addition, the predicted cone illusion during OVAR has a parallel during roll rotation as illustrated in Fig. 2B. During roll rotation, the model predicts a feeling of spiraling outward into an orbit with a roughly 0.3-m radius. It would seem that such an effect should be quite noticeable to the subject, but we have no evidence that this percept occurs. As this illusory translation percept is well established during off-vertical axis yaw rotation but is questionable during roll, the possibility should be considered that the brain processes body motions in roll and in yaw differently. A similar suggestion was made in the spatial updating study of Klier et al. (2006), who found different degrees of updating for yaw and roll rotations. Updating performance after whole body yaw movements, even when the rotation axis was perpendicular to gravity, showed larger errors and was not facilitated by gravity in the same way as roll updating. Klier et al. (2006) as well as Bockisch et al. (2005) suggested that this may be linked to the fact that yaw rotation is usually parallel to gravity and therefore stimulates the otoliths to a much lesser extent than roll head movements. Thus the fact that canal and otolith signals are rarely coupled for yaw rotations might have resulted in a system that is not well developed for these situations. An alternative explanation is that the combination of otolith signals and proprioceptive information is easier for the brain to process during roll than during OVAR. While OVAR presents a complicated, unnatural set of sensory inputs to the body, roll rotation presents a set of sensory inputs that is more easy for the brain to comprehend.

In line with other studies reporting a mismatch for the phase response in model predictions and data (Glasauer 1995; Park et al. 2006), we think that it would be premature to discard the entire model structure, solely on the absence of phase shifts. First of all, the phase lag of 15° is a relatively small effect to look for via verbal reports during dynamic stimulation. Furthermore, while the A-cluster had no significant phase shift, there was an intriguing shift in the E-cluster range under dynamic conditions. Inevitably, the computation of the responses in the dynamic condition, which requires combining retinal and tilt information, must be subject to a delay after the presentation of the visual stimulus. A further factor relates to the fact that the visual response outlasts the duration of the flash stimulus (visual persistence, see Pola 2007 for references). While subjects were instructed to report the spatial orientation of the line at the time when it was presented, the computational delay in combination with the visual persistence complicates the picture. If they are actually computing the orientation of the line a second later, their tilt angle will have changed 30° in the interval, which is the approximate amount of the shift in the E-cluster. Thus responses plotted at a body tilt of 90° would actually correspond to a body tilt of 120°. In other words, a computational delay would be expressed as a phase advance in the data. Because the phase shift in the A-cluster, tested at 0° tilt was almost negligible, it is clear that a fixed computational delay, identical for both clusters and all tilt angles, cannot explain our data. At this point, one can either simply reject the hypothesis or accept the possibility that the computational delay for the A-mode was shorter. We feel that this admittedly speculative assumption is actually not entirely unreasonable for three reasons. A smaller computational delay in the A-mode, in the order of 500 ms, would help to explain why the maximum 15° phase delay predicted by the model (see Fig. 2C) was not actually found. Furthermore, a longer computational delay in the E-mode would fit in with earlier suggestions that its responses are more cognitive (Kaptein and Van Gisbergen 2005). Finally, as the computational delay leads to a phase advance or, in other words, overestimation of tilt, a delay in the order of ~300 ms may also explain why the SBT data are shifted ~10° downward compared with the model prediction (see Fig. 10).

As the present results are based on verbal reports, a more complete picture of the mechanism at work during the dynamic SVV experiment, could be obtained by recording eye movements. In this respect, it is important to note that Merfeld et al. (2005a,b) reported that human oculomotor and perceptual responses depend on qualitatively different mechanisms, suggesting that the characteristics of the present perceptual data and the eye-movement responses are not necessarily similar.

In summary, we conclude that errors in visual verticality perception under dynamic conditions are not caused by errors in body-tilt estimation, that the egocentric-bias mechanism becomes stronger during constant-velocity roll rotation, and that disambiguation of the otolith signal shows no major errors despite the decay of canal signals.

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REFERENCES
